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NATURAL HISTORY OF PLUMMERS ISLAND, MARYLAND. XXII. BITING MIDGES (DIPTERA: CERATOPOGONIDAE). 1. INTRODUCTION AND KEY TO GENERA

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Abstract.—Wirth, Willis W., Systematic Entomology Laboratory, IIBIII, Agr. Res. Serv., USDA, c/o U.S. National Museum, Washington, D.C. 20560; Ratanaworabhan, Niphan C., Applied Scientific Research Corporation, Bangkok, Thailand; and Messersmith, Donald H., Department of Entomology, University of Maryland, College Park, Maryland 20742.—This paper is the first of a series intended as a guide to the identification, systematics, and life histories of the biting midges (Diptera: Ceratopogonidae) of Plummers Island, Maryland, and the adjacent parts of Maryland, Virginia, and the District of Columbia. A historical review is given of the Ceratopogonidae; adult anatomy, biology and immature stages, and general classification of the family are discussed. A systematic arrangement and a key for identification is presented for the 34 North American genera in four subfamilies, illustrated by seven plates of figures.

I. General Purpose of the Survey and Publications

This series of papers is made possible by a grant from the Washington Biologists' Field Club (WBFC), a nonprofit corporation of Washington area biologists dedicated to the study and preservation of the natural biota of Plummers Island in the Potomac River near Washington, D.C. The Club acquired the island and 25 adjacent acres near the Chesapeake and Ohio Canal in 1908 and maintains a rustic cabin on the island for the convenience of its members and to assist in their research. One of the principal objects of the Club is a thorough biological survey of the island and adjacent mainland property, and a less complete study, for comparative purposes, of the lower Potomac River Valley. The first Committee on Fauna and Flora was appointed in October 1902. Several formal lists of flora and fauna have been published as a series under the title "The Natural History of Plummers Island" in this journal, and members have published many other papers covering to some extent the same subject in various fields of Natural History. The present study was begun in 1976 under a WBFC grant, the objective of which is to publish a series of papers with guides to the identification, systematics and life histories of the biting midges (Diptera: Ceratopogonidae) of Plummers Island and environs (District of

Columbia, Montgomery and Prince George's counties in Maryland and Fairfax and Arlington counties and Alexandria in Virginia).

The first paper in this series will be devoted to a short general account of the anatomy, systematics, and biology of the biting midges, including their immature stages, and to a key for the identification of the genera occurring in North America. In future contributions, keys and descriptions will be given for the species found in the Washington area, and information will be summarized on their life histories.

The biting midges (Diptera: Ceratopogonidae) may be found in large numbers in nearly any aquatic or semiaquatic habitat in all regions of the world. Because of their small size (usually 1–4 mm) they have been little collected and are poorly known. Adults' habits are diverse, but females of most species are adapted to some type of blood sucking. Species of *Culicoides*, *Lasiohelea*, and *Leptoconops* suck vertebrate blood, and some are notorious pests, especially in beach or mountain resort areas. Some *Culicoides* are vectors of diseases including bluetongue of sheep, onchocerciasis of horses and cattle, horse-sickness, several human filariae, and malaria-like diseases of birds. Some *Atrichopogon* and *Forcipomyia* are ectoparasitic on large insects, whereas many genera of Ceratopogoninae (Fig. 1) are predaceous on other smaller insects. A few genera (e.g. *Dasyhelea*) are exclusively flower visiting, feeding on nectar, while many others thus supplement their diet or have non-haematophagous species. Some species are important pollinators of tropical crop plants such as cacao. The immature stages may be terrestrial under bark or on wet or damp wood (*Forcipomyia*), semiaquatic on wet alga-covered soil, wood, or rocks (*Atrichopogon*, *Dasyhelea*, etc.); in wet, decomposing plant material such as cactus stems, banana stalks, or leaf compost (*Culicoides*, etc.); or aquatic in mud or wet sand on lake, pond, or stream margins, salt marshes, tree holes, or water-holding plants (most genera).

II. Historical Background

For many years the biting midges were placed in the genus *Ceratopogon* Meigen in the family Chironomidae. The early authors followed this system, deviating only rarely to propose a new genus for some exceptionally odd form. The ceratopogonids were usually regarded at most as a subfamily of the Chironomidae until 1901 when Grassi gave them family rank, followed by Malloch in 1915. In 1926 Edwards pointed out two strong characters, the complete mouthparts and forked media, which form a clear line of division between the two families.

Beginning with the work of Kieffer (1906) the division of the genus *Ceratopogon* proceeded rapidly. During the next 20 years Kieffer proposed more than 40 new genera out of a total of 139 genus group names proposed during the entire history of the family. Of the total, 78 names sur-

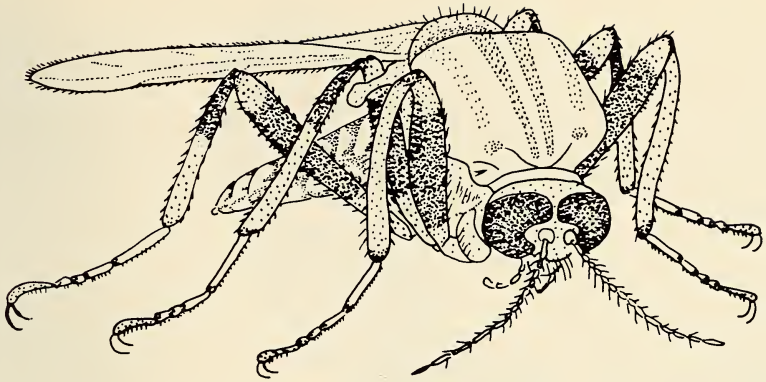

Fig. 1. General habitus of a predaceous biting midge, *Sphaeromias longipennis* (Loew) (drawn by Ethel Grogan).

vive as valid genera or subgenera, of which 28 are attributed to Kieffer. Although much maligned, Kieffer's work in the family has probably been more important than any other.

In North America Malloch (1915) broke up the genus *Ceratopogon* of earlier American workers into smaller genera, and with the help of Johannsen established the basis for the classification of the American species. In Europe Goetghebuer, Edwards, and Zilahi-Sebess set up a classification closely following Kieffer's although Edwards (1926) proposed valauble modifications of Kieffer's concepts. Elsewhere important systematic work was done by Lutz and Lane in Brazil; Carter, Ingram and Macfie, and de Meillon in Africa, Gutsevich and Remm in the USSR, Tokunaga in Japan and the Pacific, and Lee in Australia. From 1925 to 1949 Macfie served as the leading ceratopogonid authority who published a remarkable series of papers covering all parts of the world. Mayer continued the important work begun by Thienemann and Lenz on the classification of the immature stages, while Saunders showed the necessity to consider the immature stages in the Forcipomyiinae.

III. General Anatomy of the Ceratopogonidae
Fig. 2

The Ceratopogonidae are typical members of the dipteran suborder Nematocera and are closely related to the Chironomidae, with which they share many characters. In the following account material is drawn freely from the studies published by Carter, Ingram and Macfie (1920–21), Goetghebuer (1920, 1923), Kieffer (1925), Edwards (1926), Jobling (1928), Tokunaga (1937), Lee (1947), Gad (1951), Wirth (1952), and Gutsevich (1973).

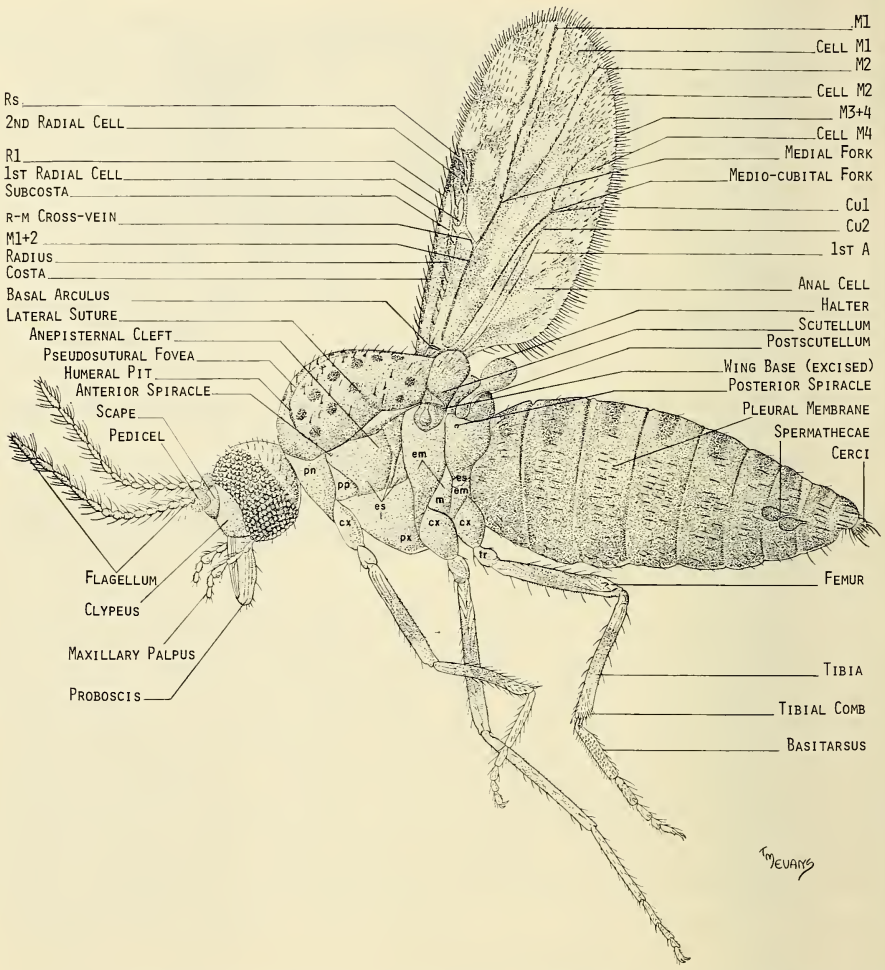

Fig. 2. *Culicoides furens* (Poey), lateral view of female, left wing and right legs removed; for explanation of abbreviations see text.

Head (Fig. 3).—Head subspherical to slightly flattened, anterior surface rather flattened and in line with anterior surface of proboscis. Dorsal surface of head consisting of broad posterior occiput and undifferentiated anterior vertex, usually with scattered setae and a row of orbital setae bent over eyes. Eyes bare or with short pubescence between the facets; contiguous above bases of antennae, or more or less separated. Two inconspicuous ocelli located on frons just above bases of antennae. Frontoclypeus present as a prominent convex sclerite between bases of antennae and proboscis.

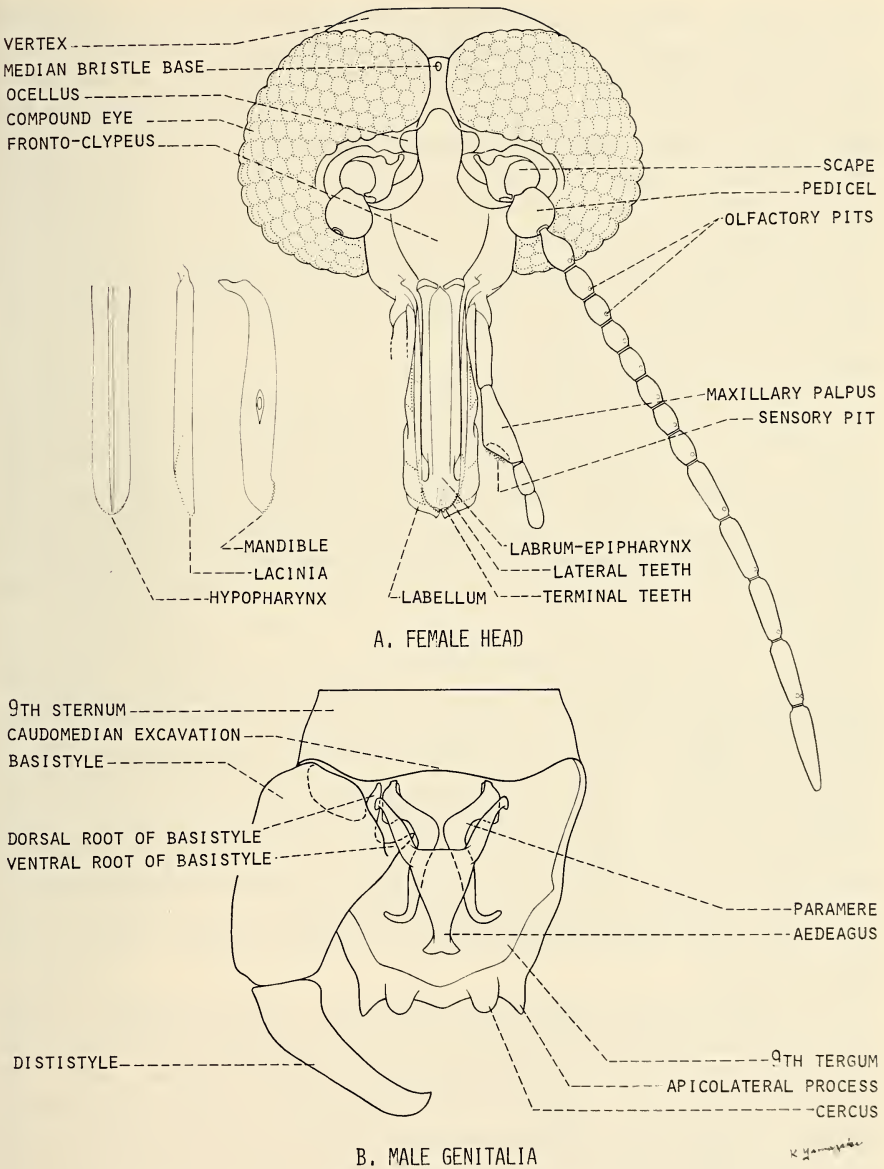

Fig. 3. *Culicoides* ssp., parts labeled. a, Female head; b, Male genitalia (after Arnaud, 1956).

Antenna usually 15-segmented, but basal segment or scape reduced to a ringlike segment in head capsule hidden by the enlarged pedicel (in using the keys, the presence of the scape is always implied and included in the count of segments). The 13 divisions of the flagellum are not true

morphological segments, but in this series of papers they are counted as segments in accordance with established custom. First 8 segments of female antenna similar and distinct from last 5, which are usually more elongated. Antennal ratio (AR) is the ratio of combined lengths of last five segments to the preceding 8. Antennal segments 4–10 of female usually short and typically bearing basal ring of long verticils and subapical pair of hyaline sensory setae; last 5 usually elongate with basal verticils not so well developed, and usually with scattered short setae and sensory setae on distal portion. Male antennae more or less plumose, pedicel much larger than in female, first 9 or 10 flagellar segments short and similar, bearing oblique whorls of long verticils, and distal 3 or 4 segments much elongated, with short verticils.

Mouthparts well developed, stronger in females than in males, fitted for piercing and sucking, and forming an elongate proboscis often as long as head. Labium fleshy with scattered setae, enclosing the other 6 parts, which are slender, distally toothed blades of subequal length. These consisting of a strong labrum, a pair of mandibles, a pair of maxillae, and a tubular sclerotized hypopharynx. Maxillary palpi usually 5-segmented in both sexes, setose; third segment usually with distal sensory organ and often swollen.

Thorax.—Usually rather broad and convex above, arched anteriorly but not greatly projecting over head, prescutellar area flattened. Pronotum divided into lateral halves by anterior development of mesonotum, partly hidden just below humeri. Mesonotum sometimes bearing small spine or tubercle in middle of anterior margin; a pair of small humeral pits located laterally near anterior margin. Pseudosutural foveae extending from the pits caudad to near ends of scutellum as a sublateral pair of slightly depressed lines. Lateral paratergites well developed in the higher Ceratopogoninae. Scutellum prominent, transverse, usually with bristles; postscutellum arched, bare, with small deep central glandular depression, but without longitudinal division.

Legs.—Legs usually rather short and stout, with characteristic modifications useful in generic differentiation. One or more pairs of femora may be swollen and bearing prominent ventral spines; tarsomeres may bear spines, or shapes of fourth or fifth tarsomeres may be characteristic. Presence of long, blunt, black, non-tapering spines or "batonnets" on ventral side of fifth tarsomere characteristic of some genera. Shape and development of the claws are extremely important in generic separation, and presence of a well-developed empodium is used to characterize the Forcipomyiinae. The most useful modifications of the fifth tarsomeres and claws are found only in the female sex, and thus the males are more difficult to characterize generically without dissecting the genitalia. Hind tarsal

ratio (abbreviated TR), often useful in specific and generic diagnoses, obtained by dividing length of basitarsus by length of second tarsomere.

Wing.—Wing moderately broad (narrower in male) with apex evenly rounded, anal lobe rarely prominent, alula usually without fringe. Wing venation extremely important in generic classification. The Tillyard modification of the Comstock-Needham system of venation is followed here (see Fig. 2). The most prominent general features are reduction of the radius to a compact anterior system, fusion of R2 + 3 with R4 + 5 to form radial sector (Rs), termination of Rl and Rs in the costa, and forking of the anterior media and its union to the radius by a crossvein. Costa long or short; one or two anterior radial cells present, one or other long or short, reduced, or absent; fork of anterior media sessile, petiolate, or interrupted beyond the crossvein. The costal ratio (CR) is obtained by dividing length of costa by wing length, measuring both from the level of the basal arculus of the wing. Posterior veins (M1, M2, M3 + 4, Cu1, Cu2, and 1st A) relatively weak. Development or reduction of the macrotrichia (long hairs) or microtrichia (microscopic spicules or setae) and presence or absence of a pattern of pigmented spots or markings are useful. In life, the wings are almost always superimposed and folded flat over the back while the insect is at rest, thus differing in habits from non-biting midges of the family Chironomidae that never superimpose their wings over the back.

Abdomen.—Female abdomen usually short and blunt, somewhat dorsoventrally flattened and terminating in a pair of cerci which are short and rounded or rarely (in *Leptoconops*) long and tapered. Genital opening in some genera flanked by modifications of the sterna or an armature of spines or hairs. Spermathecae usually strongly sclerotized, their number, size, and shape very useful in classification. In the genera of the Palpomyiini and Stenoxenini paired eversible glands open on anterior margins of certain terga; these openings marked internally by tapered internal sclerotized apodemes ("gland rods") extending from bases of terga toward base of abdomen.

Male genitalia (Fig. 3).—Male genitalia of simple nematocerous type. Rotation of eighth and succeeding segments occurring to greater or lesser degree. Ninth tergum usually an expanded plate, convex externally and hollowed out mesad, and bearing the anus flanked by pair of membranous cerci on ventromesal face. Ninth sternum usually much shorter and transverse, with aedeagus projecting caudoventrad from posterior margin and articulating with bases of basistyles. Genital appendages or claspers (parameres of Snodgrass, 1957) prominent, forcepslike and 2-segmented; basistyles usually fairly large and simple, bearing a more or less tapered, usually simple, incurved dististyle. Aedeagus usually more or less triangular or Y-shaped in ventral view, flattened and bent in gutter shape in cross

section, convex ventrally and bearing the membranous penis dorsally (internally) with its opening at or near tip of aedeagus. Parameres (claspettes of Snodgrass) typically a pair of submedian processes, often fused, usually symmetrical, articulating with bases of basistyles on dorsal side and projecting distad between aedeagus and ventral face of ninth tergum.

IV. Biology and Immature Stages of Ceratopogonidae

The first important studies on the immature stages of biting midges were made by Gercke (1883), Meinert (1886), and Mik (1888) in Europe, and Long (1902) and Johannsen (1905) in North America. Later the European workers Rieth (1915), Goetghebuer (1920), Saunders (1924), Kieffer (1925), Thienemann (1928), Lenz (1934), and Mayer (1934) brought knowledge of the European species up to date, and Malloch (1914, 1915, 1917) and Thomsen (1937) reviewed the North American species. Relatively little comprehensive work has been done in other regions of the world, although many scattered descriptions have appeared. Hennig (1950) reviewed all the published information on immature stages up to that date. Wirth (1952) published what was known of the species occurring in California, and essentially the same information was summarized in Wirth and Stone (1963).

Serious comprehensive work on the immature stages has been done only in the genera *Forcipomyia* (Saunders, 1924, 1925, 1956, 1959; Chan and LeRoux, 1965, 1970, 1971a, b, c); *Atrichopogon* (Nielsen, 1951; Ewen and Saunders, 1958); and *Culicoides* (Lawson, 1951; Kettle and Lawson, 1953; and Jamnback, 1965). Immature stages of the Forcipomyiinae are especially useful in classification and separation of closely related species, and reflect important ecological adaptations.

Egg.—Eggs differing markedly among subfamilies (Figs. 3–7); oval to elongate, often black and glossy (Leptoconopinae and Forcipomyiinae), U-shaped and enclosed in gelatinous cover in Dasyheleinae, and elongate and banana shaped in Ceratopogoninae, with conspicuous frilled collar on one end in Stenoxenini. They may be laid on a moist substrate in loose groups (*Forcipomyia*, *Culicoides*, and most other genera), or in strings or masses with gelatinous coating (*Bezzia*, *Mallochohelea*, etc.).

Larva.—Without functional spiracles. Head sclerotized (except Leptoconopinae), with strong, toothed, non-opposable mandibles; internally with conspicuous pharyngeal apparatus consisting of two strongly diverging arms and a series of combs serving to reduce and sort the food. A short collar between head and thorax; 3 thoracic and 9 abdominal segments. Four larval instars. General habitus and structure of the larva differs greatly among the subfamilies as follows:

Leptoconopinae (Fig. 4): Larva elongate and smooth, without con-

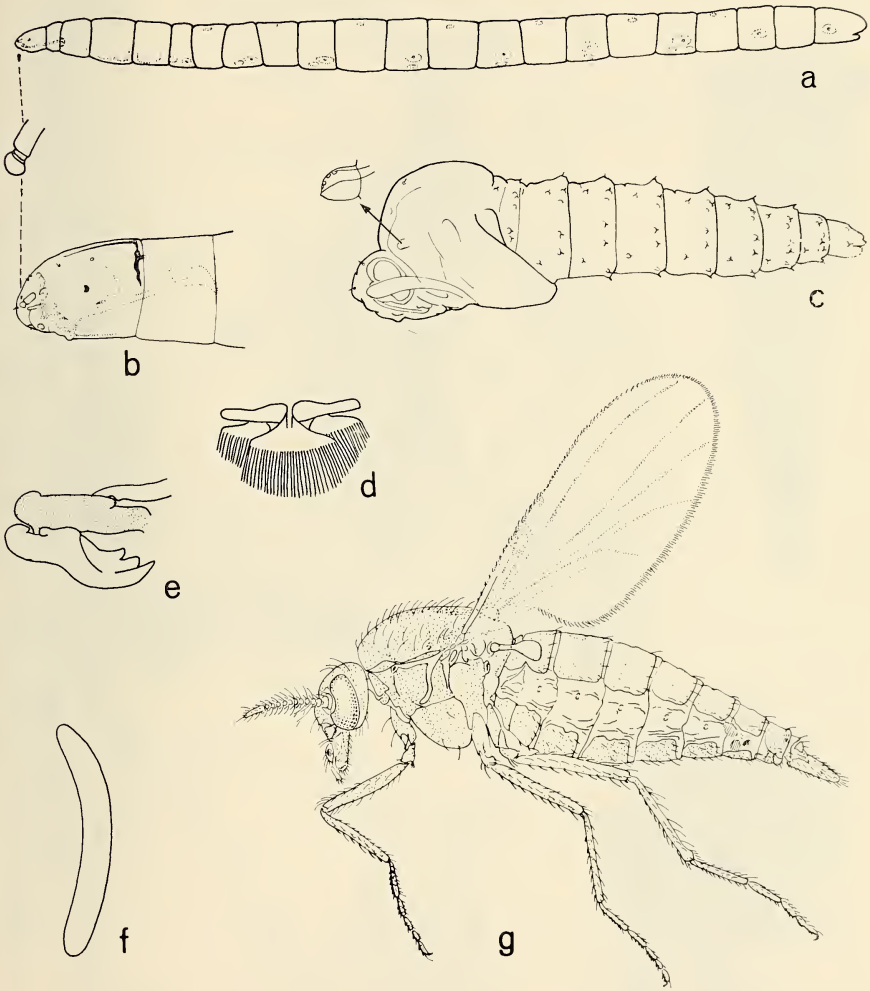

Fig. 4. Life stages of Leptoconopinae: a–f, *Leptoconops spinosifrons* (Carter) (after Laurence and Mathias); g, *Leptoconops americanus* (drawn by Ethel Grogan). a, Larva; b, Larval head; c, Pupa; d, Larval pharyngeal apparatus; e, Larval mandible; f, Egg.

spicuous setae, many segments subdivided into two subsegments; anal segment with three short lobes. Head prognathous, head capsule not fully sclerotized, with internal rodlike structures of uncertain morphology. Larval biology adapted to arid or desert areas and coastal or inland beaches in moist or wet soil which is usually hypersaline; the larvae burrow in the soil, often

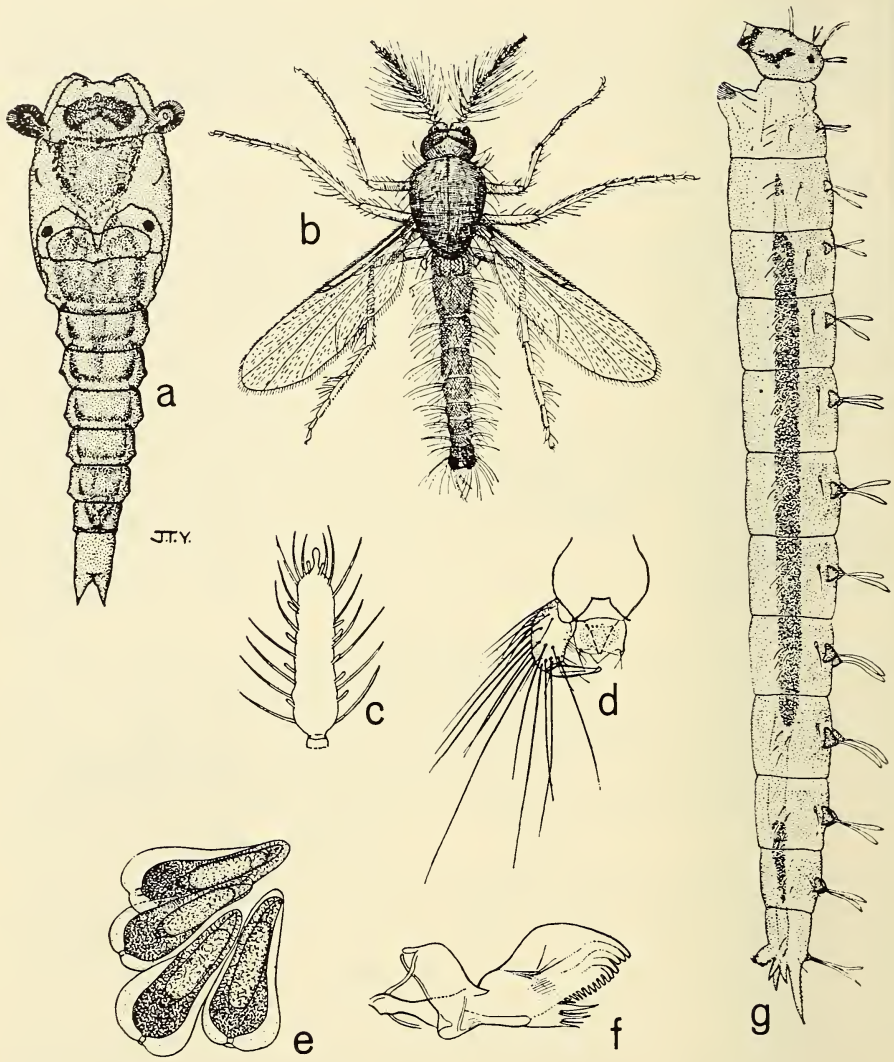

Fig. 5. Life stages of Forcipomyiinae (*Forcipomyia ingrami* Carter) (after Williams, 1944). a, Pupa; b, Adult male; c, Distal antennal segment of female; d, Male genitalia; e, Egg cluster; f, Larval mandible; g, Larva.

to great depths following moisture downward as the soil dries and cracks; some species aestivate during extremely dry periods.

Forcipomyiinae (Fig. 5): Larva often relatively stout; head usually hypognathous; body segments with conspicuous setae, often complex and set on projecting tubercles; prothorax with bilobed anterior proleg, last segment

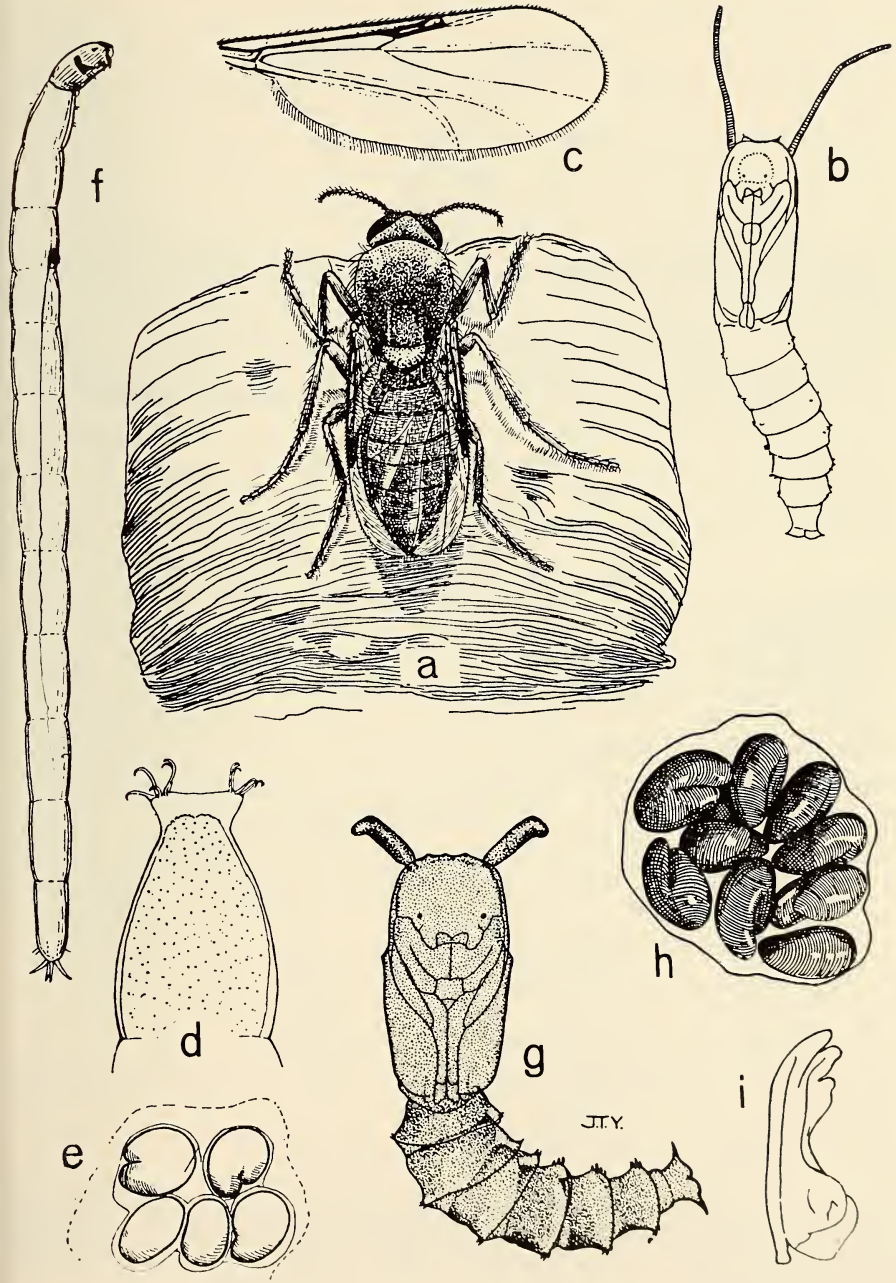

Fig. 6. Life stages of Dasyheleinae: (a–e, *Dasyhelea calvescens* Macfie; f–i, *D. hawaiiensis* Macfie) (after Williams, 1944). a, Adult female; b, g, Pupa; c, Male wing; d, Caudal end of larva; e, h, Egg cluster; f, Larva; i, Larval mandible.

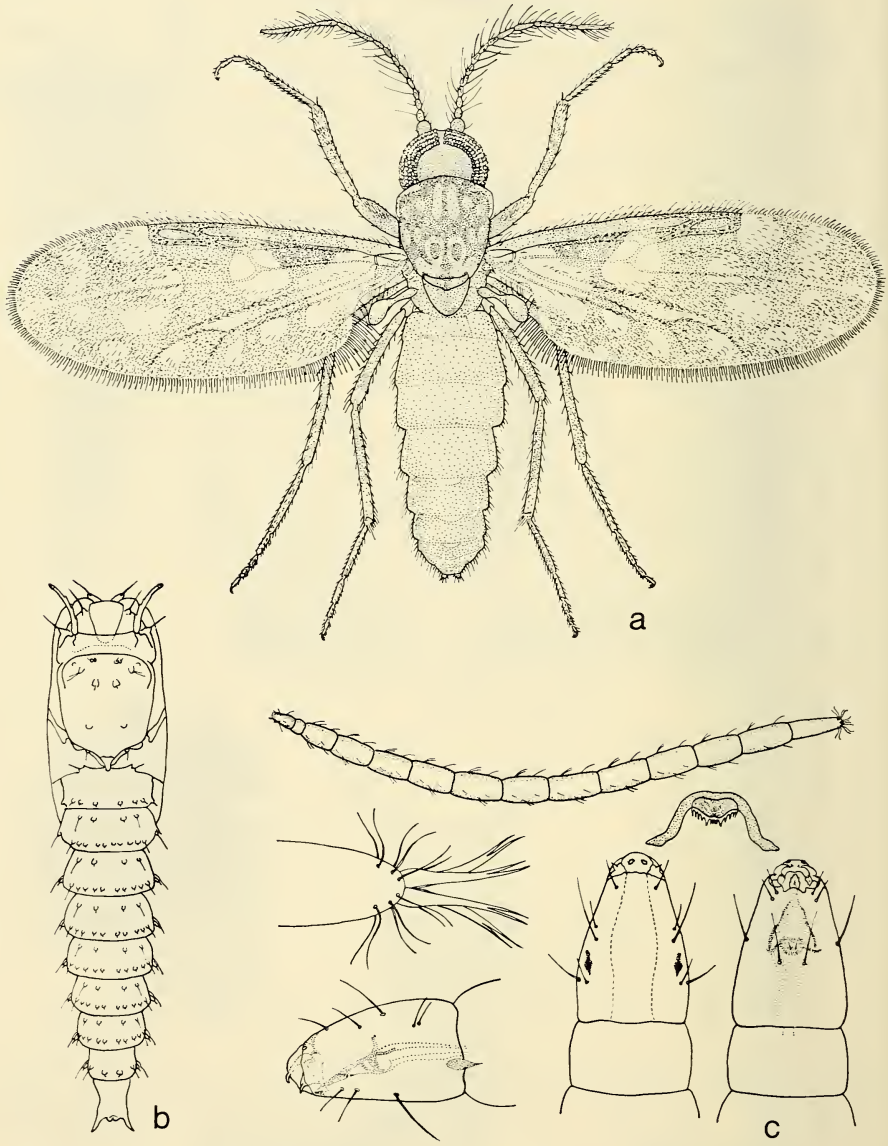

Fig. 7. Life stages of Ceratopogoninae, tribe Culicoidini: a, *Culicoides guttipennis* (Coquillett), adult female (drawn by Ethel Grogan); b–c, *C. accraensis* Carter, Ingram and Macfie (after Carter, Ingram and Macfie, 1921). b, Pupa; c, Larva, details of larval head, caudal segment.

with posterior proleg bearing conspicuous hooklets. Habits crawling; usually terrestrial in damp places such as under bark or in mosses, or semiaquatic; feeding on fungi, algae, or plant debris. In some genera last larval skin retained over posterior segments of pupa.

Dasyheleinae (Fig. 6): Larva moderately elongate, head hypognathous or intermediate in shape; body without conspicuous hairs or projections; anterior proleg absent, posterior proleg present with hooklets much as in Forcipomyiinae. Habits wriggling chironomid-like, not free swimming; usually living in blanket algae or algae on mud or wet rocks at stream or pond margins; often in restricted habitats such as rock pools, tree holes and sap flows. Feeding habits usually phytophagous on algae.

Ceratopogoninae (Fig. 7): Larva with distinctive, elongate, eellike form and prognathous, somewhat elongated head. Body hairs minute except on last segment; cuticle smooth, whitish or translucent; no prolegs (except first instar of some *Culicoides*). Habits ranging from semiaquatic, burrowing in moist soil or sphagnum mats, to fully aquatic and free swimming; some genera in benthos and plankton of large lakes and streams. Feeding habits usually carnivorous.

Pupa.—Appearance relatively uniform and characteristic; yellowish brown to blackish in color; usually rather conical in form, body more or less compact, stout anteriorly with pair of prothoracic respiratory horns of diverse structure; last segment bearing pair of pointed, apicolateral processes. Structural details (Figs. 4–7) of respiratory horn, operculum (vertex), tubercles bearing spines or setae, and apicolateral processes of abdomen usually of great diagnostic value for taxa at all levels. Movement usually possible by twisting movements of abdomen but not true swimming; air breathing by anterior horns, aquatic forms hanging at water surface by non-wettable horns, supported by air bubble beneath wing cases.

V. Systematic Arrangement of the North American Genera of Ceratopogonidae

Subfamily Leptoconopinae Noé

Genus *Leptoconops* Skuse (23 North American species)

Subfamily Forcipomyiinae Lenz

Genus *Atrichopogon* Kieffer (27 species)
Genus *Forcipomyia* Meigen (73 species)

Subfamily Dasyheleinae Lenz

Genus *Dasyhelea* Kieffer (29 species)

Subfamily Ceratopogoninae Newman
Tribe Culicoidini Kieffer

Genus *Paradasyhelea* Macfie (1 species)
Genus *Culicoides* Latreille (137 species)

Tribe Ceratopogonini Newman

Genus *Alluaudomyia* Kieffer (8 species)
Genus *Brachypogon* Kieffer (1 species)
Genus *Ceratoculicoides* Wirth and Ratanaworabhan (3 species)
Genus *Ceratopogon* Meigen (4 species)
Genus *Isohelea* Kieffer (3 species)
Genus *Rhynchohelea* Wirth and Blanton (1 species)

Tribe Stilobezziini Wirth

Genus *Echinohelea* Macfie (1 species)
Genus *Monohelea* Kieffer (16 species)
Genus *Parabezzia* Malloch (14 species)
Genus *Serromyia* Meigen (3 species)
Genus *Stilobezzia* Kieffer (18 species)

Tribe Heteromyiini Wirth

Genus *Clinohelea* Kieffer (7 species)
Genus *Heteromyia* Say (2 species)
Genus *Neurobezzia* Wirth and Ratanaworabhan (1 species)
Genus *Neurohelea* Kieffer (2 species)
Genus *Pellucidomyia* Macfie (1 species)

Tribe Sphaeromiini Newman

Genus *Jenkinshelea* Macfie (4 species)
Genus *Johannsenomyia* Malloch (2 species)
Genus *Macropeza* Meigen (1 species)
Genus *Mallochohelea* Wirth (11 species)
Genus *Nilobezzia* Kieffer (4 species)
Genus *Probezzia* Kieffer (19 species)
Genus *Sphaeromias* Curtis (1 species)

Tribe Palpomyiini Enderlein

Genus *Bezzia* Kieffer (43 species)
Genus *Pachyhelea* Wirth (1 species)
Genus *Palpomyia* Meigen (25 species)

Tribe Stenoxenini Coquillett

Genus *Paryphoconus* Enderlein (1 species)
Genus *Stenoxenus* Coquillett (1 species)

VI. General Classification of the Ceratopogonidae

Leptoconopinae.—There is general agreement that the Leptoconopinae stand somewhat apart from the other ceratopogonids and some modern workers have proposed separate family status for them (Zilahi-Sebess, 1960; Krivosheina, 1962; Remm, 1975). The wide separation of the eyes in both sexes, 13- or 14-segmented female antennae, pale wings without macrotrichia, absence of the r-m crossvein and extreme shortening of the radial system into a compact stigma, lengthening of the female cerci into tapering lamellae in most, articulated tooth at the tip of the male dististyle, and extreme reduction of the larval head capsule are unusual in the Ceratopogonidae. Great as these differences are, we do not believe the Leptoconopinae are distinctive enough from other ceratopogonids to warrant family recognition.

Forcipomyiinae.—Classification of the Forcipomyiinae is more advanced than that of any other group, thanks almost entirely to fine work on the immature stages by Saunders. Chan and LeRoux (1965, 1970, 1971a, b, c) have continued more recently in Saunders' tradition in describing several new subgenera of *Forcipomyia*, emphasizing all the while the importance of immature stages in the classification of this subfamily. Dessart (1963), working on cacao pollination in Zaire, brought the African species into the modern classification. Remm (1961a, b, 1962, 1969, 1974a, b), in Estonia, has made similar advances in revising the Palaearctic species that are found in the Soviet Republics. Larvae, pupae, male genitalia, and habits offer excellent characters in the Forcipomyiinae, but the females are more difficult to classify.

Dasyheleinae.—In some ways the genus *Dasyhelea* is as distinct as *Leptoconops*, although in general its characters are intermediate between those of the Forcipomyiinae and Ceratopogoninae, as the older workers recognized when they proposed the term "Ceratopogoinae Intermediae" for these midges (Rieth, 1915). The distinctive sculpturing of the antennal segments, the characteristic flattening of the head with closely contiguous eyes and reduced mouthparts not adapted for bloodsucking in the female, the asymmetrical male parameres, and the wriggling type of larva with only the posterior proleg present, serve to place this genus in a subfamily of its own.

Ceratopogoninae.—We recognize seven tribes in this subfamily, as listed in our synopsis. The genera placed in the tribe Culicoidini appear to be as primitive and nonspecialized as any in the family, and along with those in

the subfamilies Dasyheleinae and Leptoconopinae and the tribe Ceratopogonini may give us more clues to the ancestral lineage than other sections of the family. We believe it is significant that the annectant genera *Paradasyhelea* Macfie and *Austroconops* Wirth and Lee from Australia, New Zealand, and Patagonia belong in the Culicoidini. Classification of the important blood-sucking genus *Culicoides* is still poorly understood, for although many subgenera have been proposed, most of them are valid only in one particular geographic region or another and must be revised or supplemented to bring the other species of the world into the system.

The tribe Ceratopogonini has been relatively neglected and needs a good contemporary revisionary study. Distinctions between this tribe and the Stilobezziini are not clear-cut and good synapomorphies have not been worked out in either tribe. Classification of these tribes, as for others in the Ceratopogoninae, has been seriously hindered by lack of good characters in the immature stages. Generic characters have been found mainly in the female wings, fifth tarsomeres and claws, and the male genitalia.

Tokunaga (1962) in his revision of the New Guinea "Palpomyiinae" adopted a conservative viewpoint with respect to these large predaceous midges, using the traditional characters of number of radial cells in the wing and armature of the femora. A much better classification of genera can be secured, however, by first separating those whose females have internal sclerotized gland rods and eversible glands on the abdomen. These genera, comprising the tribes Stenoxenini and Palpomyiini, are also characterized by the females having cordiform fourth tarsomeres, fifth tarsomeres without true batonnets, and claws simple and equal. Wirth (1962) published this separation in 1962, when he gave a key and suggested an arrangement for the remaining genera, which he placed in two tribes, the Heteromyiini and Sphaeromiini.

In the tribe Heteromyiini, the female claws are unequal, at least on the hind pair of legs; the fifth tarsomere does not bear ventral batonnets and those on the fore legs are often inflated, while the fourth tarsomere is sometimes divided into spinose bifid lobes. Larger genera of the tribe Heteromyiini are *Clinohelea* Kieffer and *Neurohelea* Kieffer, and in the tropics are such bizarre forms as *Heteromyia* Say, *Pellucidomyia* Macfie, and *Tetrabezzia* Kieffer.

In the genera of the tribe Sphaeromiini are found the most striking developments of the secondary sexual characters of the female tarsi. Common to all these genera is the development of specialized, stout, blunt, black, ventral spines on the fifth tarsomere which Kieffer called "batonnets." Among genera, these are arranged differently. Other convenient characters used for generic separation are the equal or unequal size of the female claws, location of the basal tooth on the internal or external side of

each claw, and the shape of the claw, straight, bent, or curved. The length of the costa is a more valuable character than the presence of one or two radial cells, and the armature of the femur is not often useful above the species level. In addition, certain genera characteristically have dull pollinose integument, especially on the thorax, whereas others are shining midges. In the tribe Sphaeromiini, the pupae of some genera have unusual ventral glandular discs on certain abdominal segments which appear to be used to attach the pupa fast to emergent vegetation or other objects above the water level preparatory to eclosion. This development probably is associated with the preferred larval habitat, larger streams with fluctuating water level or lakes with considerable wave action on the shores.

VII. Key to North American Genera of Ceratopogonidae (Adults, Primarily for Females)

North American genera not occurring in the Washington, D.C. area are bracketed in this key.

1. Wing with crossvein r-m absent (Fig. 8); wing without macrotrichia (Fig. 8); female antenna with 13 or 14 segments (Fig. 14, flagellum) (LEPTOCONOPINAE) [*Leptoconops* Kieffer]
– Wing with crossvein r-m present (Fig. 9); wing with (Fig. 10) or without macrotrichia; female antenna with 15 segments (Fig. 15, flagellum) 2
2. Empodium well developed, at least in female, claws markedly curved (Figs. 18, 20); wing usually with numerous macrotrichia (Figs. 9–10) (FORCIPOMYIINAE) 3
– Empodium smaller or vestigal (Fig. 24); claws usually gently curved (Fig. 48) but in some females of specialized raptorial form (Fig. 70); wing usually with microtrichia less numerous or absent 4
3. Costa reaching well beyond middle of wing; second radial cell longer than first and usually broad; microtrichia of wing large and conspicuous, macrotrichia when present scattered, suberect, not scalelike; fringe of posterior border of wing simple, a single row of alternating short and very short, simple, straight hairs (Fig. 9) *Atrichopogon* Kieffer
– Costa short or long; second radial cell if long is narrow; microtrichia minute, macrotrichia more abundant, covering greater part of wing, sloping, often scalelike; fringe more complex, not a single row of setae (Fig. 10) *Forcipomyia* Meigen
4. Antennal segments sculptured, at least in male (Fig. 34); first radial cell nearly or completely closed, second closed or square

ended, usually ending near middle of wing (Fig. 29); female claws small and equal (Fig. 48); eyes very finely pubescent (DASYHELEINAE) *Dasyhelea* Kieffer

– Antennal segments not sculptured; one or both radial cells well developed, second not markedly square ended, usually ending past middle of wing (except in *Paradasyhelea*); eyes usually bare (CERATOPOGONINAE) 5

5. Media petiolate, forking distad of level of r-m crossvein (Fig. 77) (in *Echinohelea*, with spinose legs, media forks just at crossvein (Fig. 81)); M2 sometimes obsolescent basally 6

– Media sessile, forking at or proximad of level of crossvein (Fig. 147); M2 nearly always complete 19

6. Claws of both sexes small, equal and simple (Fig. 45); macrotrichia of wing usually abundant; two more or less equal radial cells usually present; humeral pits prominent (CULICOIDINI) 7

– Claws of female usually large, equal or unequal (Fig. 68), those of male smaller and equal; macrotrichia less numerous or absent; one or two radial cells, second usually larger than first (Fig. 78); humeral pits less prominent or absent 8

7. Two radial cells present, usually well formed, rarely obliterated (Fig. 31); costa usually extending past middle of wing; wing usually adorned with pale or dark spots (Fig. 31); palpus 5-segmented (Fig. 40); female mouthparts usually fitted for bloodsucking with toothed mandibles (Fig. 38) *Culicoides* Latreille

– Both radial cells completely obliterated, costa short, not reaching middle of wing; wing not conspicuously adorned (Fig. 30); palpus 3- or 4-segmented; mouthparts reduced, female mandibles not toothed [*Paradasyhelea* Macfie]

8. Second radial cell small, not or little longer than first, one or both radial cells may be closed (in *Alluaudomyia* first radial cell closed, second long, macrotrichia usually numerous, wing usually with small black spots (Fig. 53)); eyes usually pubescent; wing often milky (CERATOPOGONINI) 9

– Second radial cell long, much longer than first, which may be obliterated (Fig. 77); wing hyaline or with dark pattern, not milky; eyes usually bare (STILOBEZZIINI) 14

9. Wing with both radial cells open and complete (Fig. 56) 10

– Wing with at least one radial cell obsolete (Fig. 57) 11

10. Costa extending to well past middle of wing, radial cells more elongate (Fig. 55); three large spermathecae present (Fig. 72); male parameres separate (Fig. 74) *Ceratopogon* Meigen

– Costa extending to about middle of wing; radial cells short with adjacent veins thickened (Fig. 56); one or two large spermathecae present; male parameres usually broadly fused proximally *Isohelea* Keiffer

11. Female antenna 14-segmented, very short, with segments moniliform (Fig. 64); proboscis stout and truncate (Fig. 59); palpus stout, third segment greatly broadened (Fig. 61); radial cells absent, vein M1 obsolete distally, M2 absent (Fig. 58) [*Rhynchohelea* Wirth and Blanton]

– Female antenna 15-segmented, elongate with slender segments (Fig. 66); radial cells and media various 12

12. Female claws unequal, at least on hind legs (Fig. 68); wing pattern of small isolated black spots or streaks (Fig. 53) *Alluaudomyia* Kieffer

– Female claws equal on all legs; wing pattern present or absent 13

13. Female claws small to large, but of same length on all legs (Fig. 70); one spermatheca; eyes contiguous; radial cells obsolete; male apicolateral processes absent *Brachypogon* Kieffer

– Female claws small on one pair of legs, usually hind legs (Fig. 67); 2 spermathecae; eyes broadly separated; first radial cell closed, second present but small (Fig. 57); male ninth tergum with well developed apicolateral processes *Ceratoculicoides* Wirth and Ratanaworabhan

14(8). Femora armed with one or more stout ventral spines, at least on one pair of legs (Figs. 91, 94) 15

– Femora not armed with stout ventral spines 17

15. All femora armed with numerous spines, at least in male sex, these not confined ventrally (Fig. 94); two well developed radial cells (Fig. 81); male antenna not plumose, last five segments elongated as in female; reddish yellow pruinose species *Echinohelea* Macfie

– Only hind or fore femur armed with ventral spines; one or two radial cells; male antenna plumose; color various 16

16. Fore femur slender and unarmed, hind femur greatly swollen and arcuate, and armed with numerous ventral spines (Fig. 91); two well developed radial cells (Fig. 80); shining black species *Serromyia* Meigen

– Fore femur armed with 1–2 ventral spines; hind femur slender and unarmed; first radial cell obliterated (Fig. 77); pollinose yellow or brownish species *Stilobezzia* subgenus *Eukraiohelea* Ingram and Macfie

17. One radial cell present; female costa long, extending past end

of vein R4 + 5 and ending nearly at wing tip (Fig. 82); palpus with segments four and five fused (Fig. 86) *Parabezzia* Malloch

– Two radial cells present; costa shorter, not extending past end of vein R4 + 5 and not ending nearly at wing tip (Fig. 78); palpus 5-segmented (Fig. 87) 18

18. Female claws usually large and unequal on all legs (Fig. 95) *Stilobezzia* Kieffer

– Female claws equal on four anterior legs, hind leg with one long talon and with or without a second or shorter claw *Monohelea* Kieffer

19(5). Fifth tarsomeres of female armed ventrally with stout, black, blunt spines (batonnets) (Fig. 138); female abdomen without internal sclerotized gland rods; eighth segment of female often with ventral pair of hair tufts near gonopore (Fig. 141) (SPHAEROMIINI) 20

– Fifth tarsomeres of female unarmed or provided with only slender, sharp-tipped spines (Fig. 121); if tarsi armed, female abdomen with internal sclerotized gland rods (Fig. 162); eighth segment of female without ventral hair tufts near gonopore 26

20. Female tarsal claws unequal on four posterior legs, equal on fore legs (Fig. 134); femora unarmed (abdomen petiolate; eighth segment of female abdomen with ventral pair of hair tufts; mesonotum with microtubercles bearing appressed setae (Fig. 132); costa extending to about 0.8 of wing length; usually two radial cells (Fig. 123)). *Johannsenomyia* Malloch

– Female tarsal claws equal on all legs; femora armed or unarmed 21

21. Female claws with slender internal basal barb and gently curved distally (Fig. 137); costa extending nearly to wing tip (Fig. 125) *Sphaeromias* Kieffer

– Female claws with blunt external basal tooth at least on one pair of legs and usually straight or flattened distally (Fig. 138); costa various 22

22. Costa short, extending to about 0.8 of wing length (Fig. 122) 23

– Costa long, extending nearly to wing tip (CR over 0.87) (Fig. 126) 24

23. Body slender; mesonotum shining yellow to black with little or no pollen; femora armed or unarmed; two radial cells present (Fig. 122); male genitalia with well developed basistyle and articulated dististyle (Fig. 142) *Mallochohelea* Wirth

– Body stout; mesonotum dull, usually with dense whitish to grayish pollen; femora ventrally and tibiae dorsally armed

with numerous fine sharp spines; one or two radial cells present (Fig. 124); male genitalia with short, stout basistyle fused with budlike dististyle (Fig. 140) *Nilobezzia* Kieffer

24. Wing broad with large angular anal lobe (Fig. 128) *Jenkinshelea* Macfie

– Wing not unusually broad; anal lobe not angularly developed 25

25. Female claws short and curved, sharp pointed, each with inconspicuous external basal tooth (Fig. 145); mesonotum without strong erect bristles [*Macropeza* Meigen]

– Female claws longer, straighter, and somewhat flattened distally, each with strong, blunt, external basal tooth; mesonotum with strong erect bristles *Probezzia* Kieffer

26(19). Claws of female usually unequal (at least on hind leg), or a single claw with basal tooth (Figs. 112, 114); female abdomen without internal sclerotized gland rods (HETEROMYIINI) 27

– Claws of female equal on all legs (Fig. 159); female abdomen usually with one or more pairs of internal sclerotized gland rods (Fig. 162) 31

27. Costa greatly prolonged beyond tip of vein Rs (Figs. 100–101) 28

– Costa not prolonged beyond tip of vein Rs (Figs. 102–104) 29

28. Two radial cells present (Fig. 101); claws equal on all legs; fifth tarsomere of fore leg somewhat inflated (Fig. 111) *Neurohelea* Kieffer

– One radial cell present (Fig. 100); claws equal on fore and mid legs, unequal on hind leg; fifth tarsomere of fore leg not inflated (Fig. 113) [*Neurobezzia* Wirth and Ratanaworabhan]

29. Fourth tarsomere cylindrical or cordiform but not divided into spinose bifid lobes; claws equal on fore and mid legs, with one long talon and much smaller second claw (Fig. 114) 30

– Fourth tarsomere of mid and hind legs ending in two bifid lobes armed with spines, cordiform on fore leg; claws equal on fore leg, unequal on mid and hind legs (Fig. 112) *Clinohelea* Kieffer

30. Fore femur greatly swollen and armed ventrally, the tibia arcuate (Fig. 110); fourth tarsomeres of fore and mid legs cordate (Fig. 114); one or two radial cells; wing fasciate (Fig. 103); mesonotum more or less shining *Heteromyia* Say

– Fore femur slender, unarmed, the tibia normal; fourth tarsomeres not cordate; one radial cell (Fig. 102); wing milky white, mesonotum whitish pollinose [*Pellucidomyia* Macfie]

31(26). Body unusually slender and dorsoventrally flattened; one very narrow radial cell usually extending to wing tip (Fig. 150); r-m crossvein often very short, cell between base of R and

M very narrow or even obliterated (Fig. 151); eyes broadly separated (Fig. 152); eighth abdominal segment of female narrow distally with genital sclerotization; legs long and slender, with fine setae; femora unarmed, claws very short (Fig. 160) (STENOXENINI) 32

– Body not unusually slender or dorsoventrally flattened; one or two radial cells, if cells narrow costa not extending nearly to wing tip; r-m crossvein longer, cell between R and M well formed and not very narrow (Figs. 147–149); eyes narrowly to moderately separated; eighth abdominal segment of female not modified; legs usually not extremely long nor hairy; femora often armed; claws usually moderately long (Figs. 159–161) (PALPOMYIINI) 33

32. Thorax broadly rounded anteriorly, without median spine; female wing with vein M2 strikingly elbowed at base (Fig. 151); palpus 4-segmented; two spermathecae present; male parameres fused apically [*Stenoxenus* Coquillett]

– Thorax narrowed in front, more or less conical with erect anteromedian spine (Fig. 154); female with vein M2 not elbowed at base (Fig. 150); palpus 5-segmented; one spermatheca present; male parameres separate apically [*Paryphoconus* Enderlein]

33. Two radial cells 34

– One radial cell (Fig. 149) *Bezzia* Kieffer

34. Hind femur greatly swollen; femora unarmed (Fig. 158) [*Pachyhelea* Wirth]

– Hind femur not greatly swollen, if moderately swollen at least one pair of femora armed with ventral spines; fore femur often swollen (Fig. 157) *Palpomyia* Meigen

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Figs. 8–28. Chracters of Leptoconopinae and Forcipomyiinae (Figs. 8–164 drawn by N. C. Ratanaworabhan). *Leptoconops americanus* Carter: 8, 11, 13, 14, 16, 19, 24, 28. *Forcipomyia bipunctata* (Linnaeus): 10, 12, 15, 17, 18, 21, 22, 23, 26. *Forcipomyia glauca* Macfie: 25. *Atrichopogon levis* (Coquillett): 9, 20, 27.

Figs. 29–52. Characters of Dasyheleinae and Ceratopogoninae (Culicoidini). *Dasyhelea grisea* (Coquillett): 32, 34, 42, 46, 48, 51. *Dasyhelea mutabilis* (Coquillett): 29. *Paradasyhelea minuta* Wirth and Lee: 30, 36, 37, 39, 43, 47, 52. *Culicoides yukonensis* Hoffman: 31, 33, 35, 38, 40, 41, 44, 45, 49, 50.

Figs. 53–76. Characters of Ceratopogoninae (Ceratopogonini). *Alluaudomyia bella* (Coquillett): 53, 68, 73, 76. *Brachypogon paraensis* Wirth and Blanton: 54, 60, 63, 66, 70, 71, 75. *Ceratoculicoides longipennis* Wirth: 57, 62, 67. *Ceratopogon culicoidithorax* Hoffman: 55, 69, 72, 74. *Isohelea stigmalis* (Coquillett): 56, 65. *Rhynchohelea monilicornis* Wirth and Blanton: 58, 59, 64.

Figs. 77–99. Characters of Ceratopogoninae (Stilobezziini). *Stilobezzia elegantula* (Johannsen): 77. *Stilobezzia festiva* Kieffer: 78, 88, 90, 95. *Echinohelea lanei* Wirth: 81, 83, 92, 94, 96, 97. *Monohelea hieroglyphica* Kieffer: 79, 87, 89, 93, 98, 99. *Parabezzia petiolata* Malloch: 82, 85, 86. *Serromyia femorata* (Meigen): 80, 84, 91.

Figs. 100–121. Characters of Ceratopogoniae (Heteromyiini). *Clinohelea bimaculata* (Loew): 104, 109, 112, 119, 120. *Heteromyia fasciata* (Say): 103, 105, 106, 107, 108, 110, 114. *Pellucidomyia lanei* Wirth: 102, 115, 116. *Neurobezzia granulosa* (Wirth): 100, 113, 121. *Neurohelea nigra* Wirth: 101, 111, 117, 118.

Figs. 122–146. Characters of Ceratopogoninae (Sphaeromiini). *Jenkinshelea magnipennis* (Johannsen): 128, 135. *Johannsenomyia argentata* (Loew): 123, 129, 132, 133, 134, 136, 144, 146. *Macropeza natalensis* (de Meillon): 127, 130, 145. *Mallochohelea albibasis* (Malloch): 122, 142, 143. *Nilobezzia schwarzii* (Coquillett): 124, 138, 140. *Probezzia pallida* Malloch: 126, 139, 141. *Sphaeromias longipennis* (Loew): 125, 131, 137.

Figs. 147–164. Characters of Ceratopogoninae (Palpomyiini and Stenoxenini). *Bezzia setulosa* (Loew): 149, 153, 163, 164. *Pachyhelea pachymera* (Williston): 148, 158, 161. *Palpomyia plebeia* (Loew): 147, 155, 157, 159, 162. *Stenoxenus coomani* Seguy: 151, 152, 156, 160. *Paryphoconus angustipennis* Enderlein: 150, 154.


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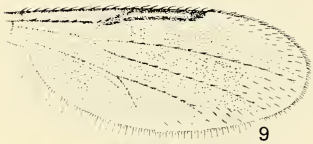
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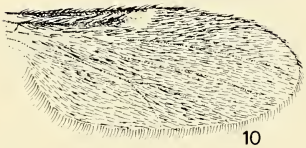
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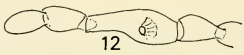
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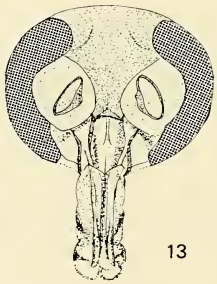
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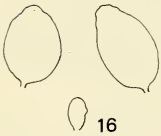
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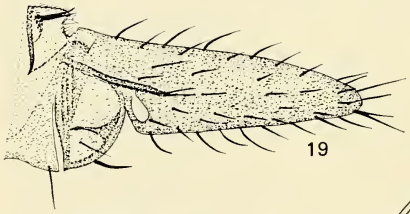
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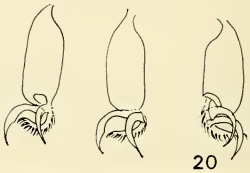
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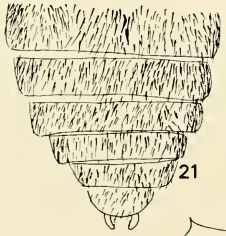
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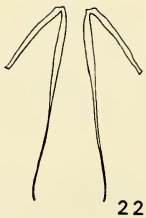
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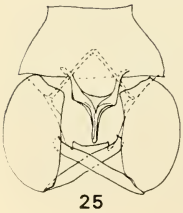
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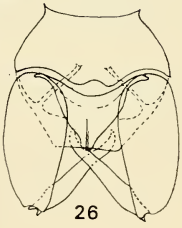
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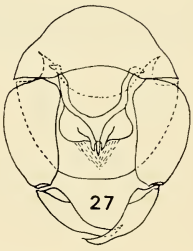
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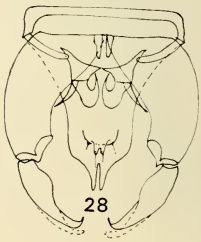
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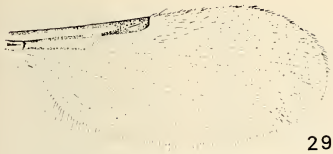
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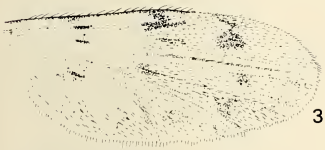
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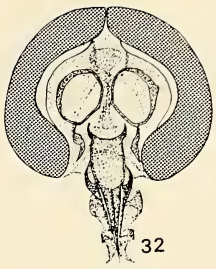
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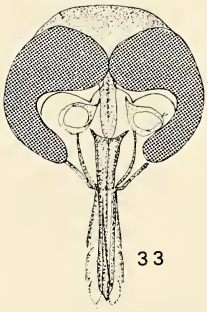
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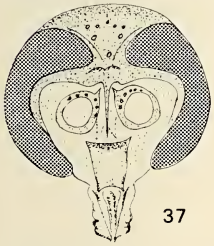
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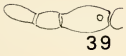
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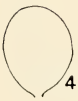
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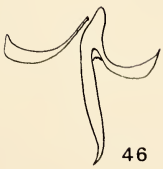
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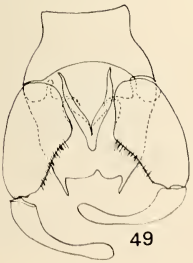
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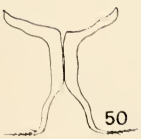
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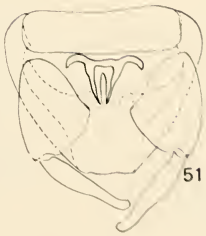
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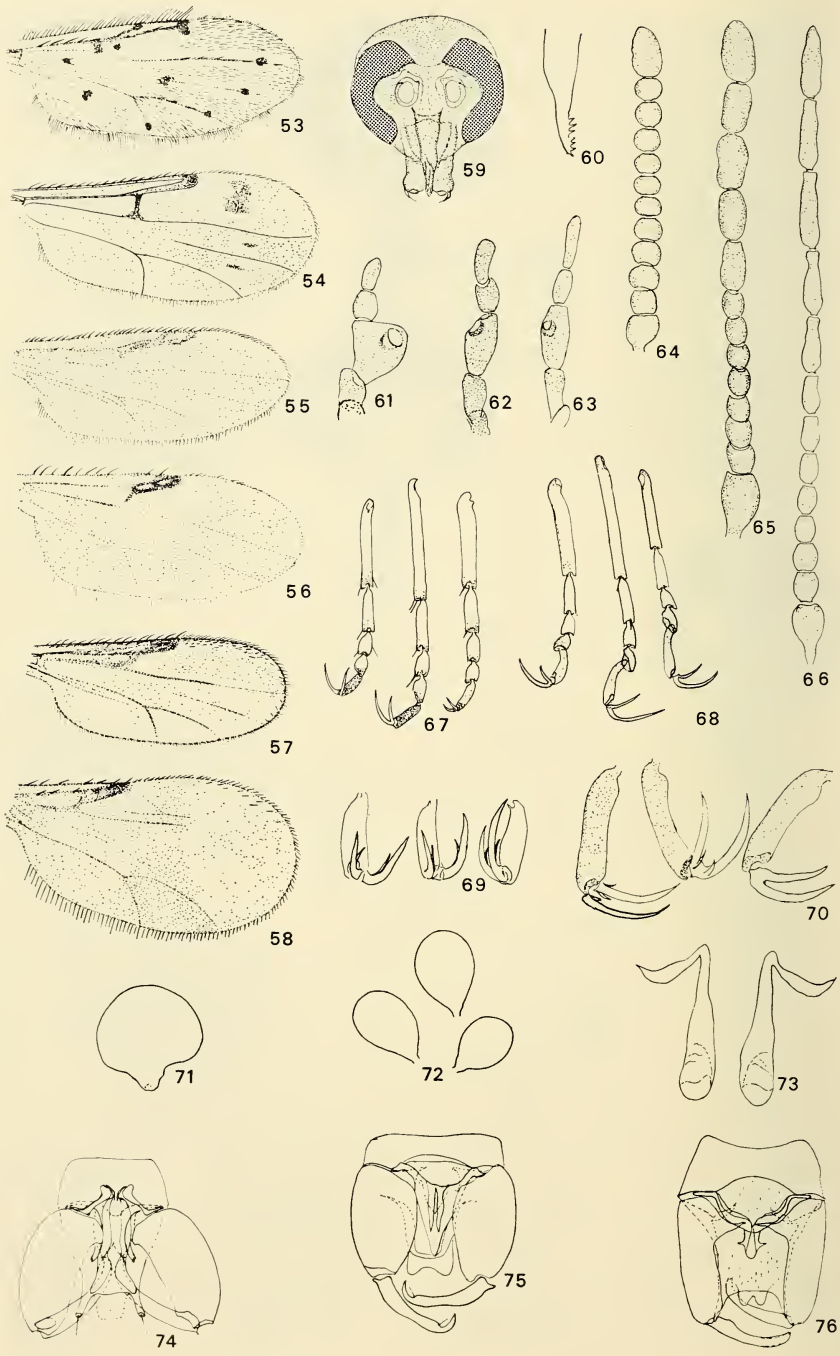
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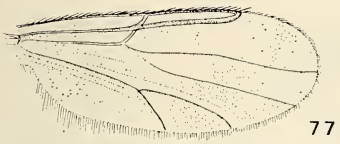
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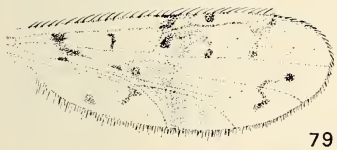
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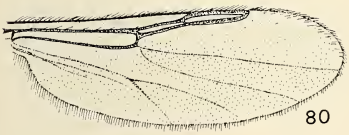
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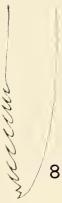
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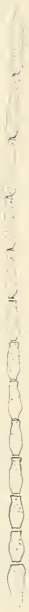
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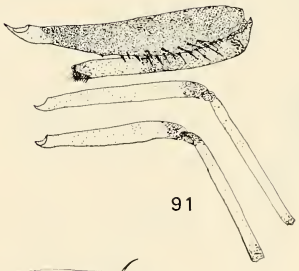
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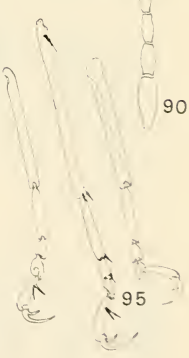
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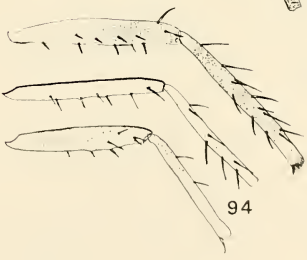
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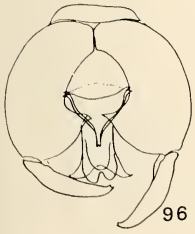
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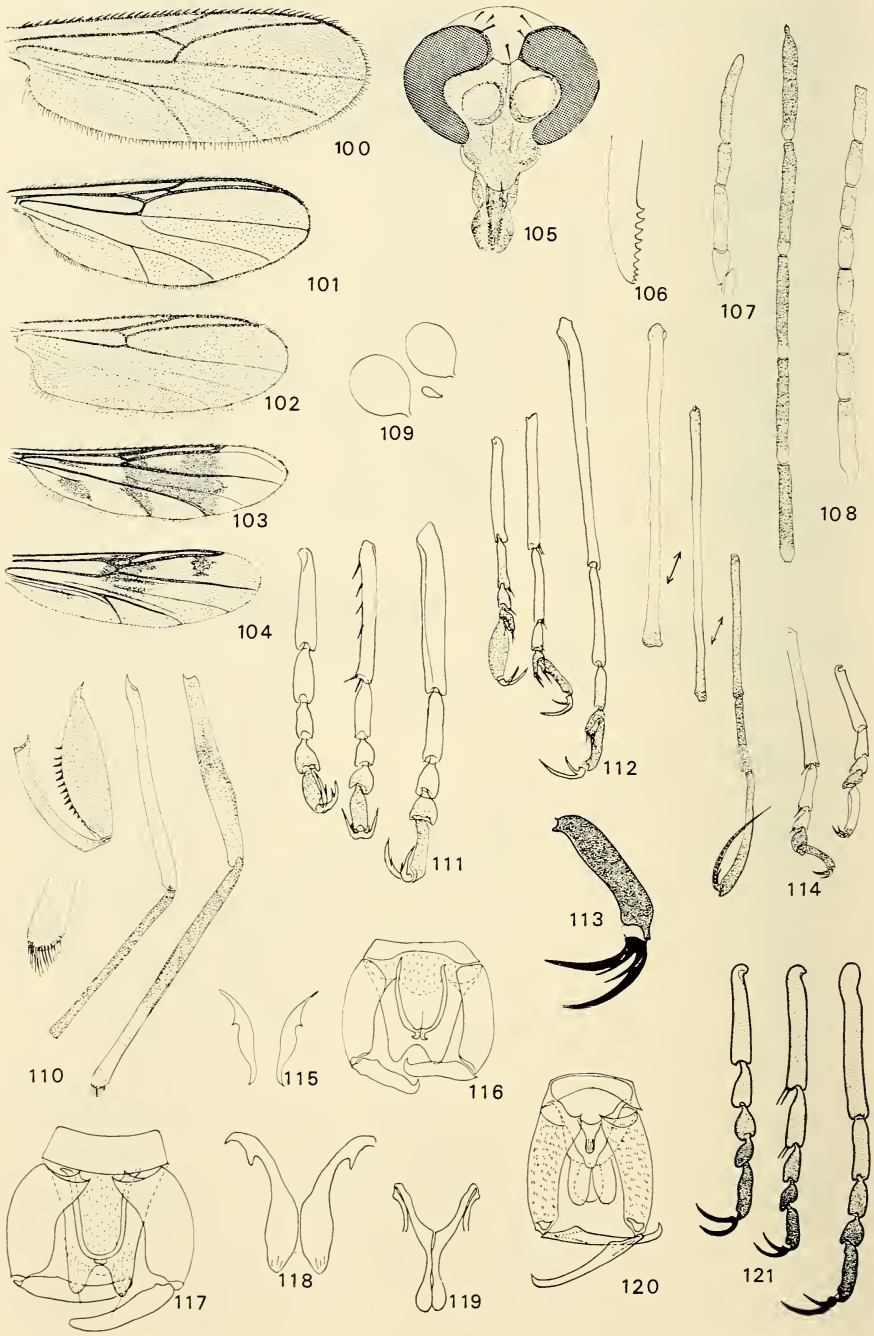
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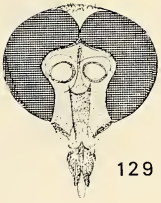
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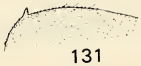
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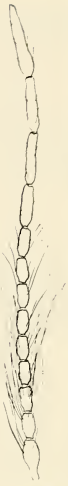
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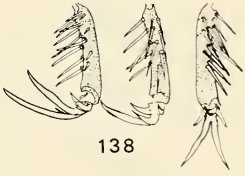
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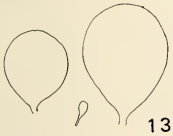
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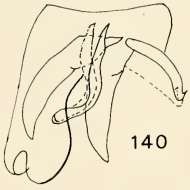
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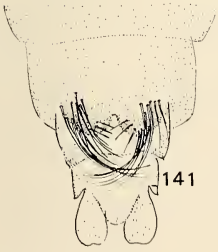
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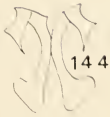
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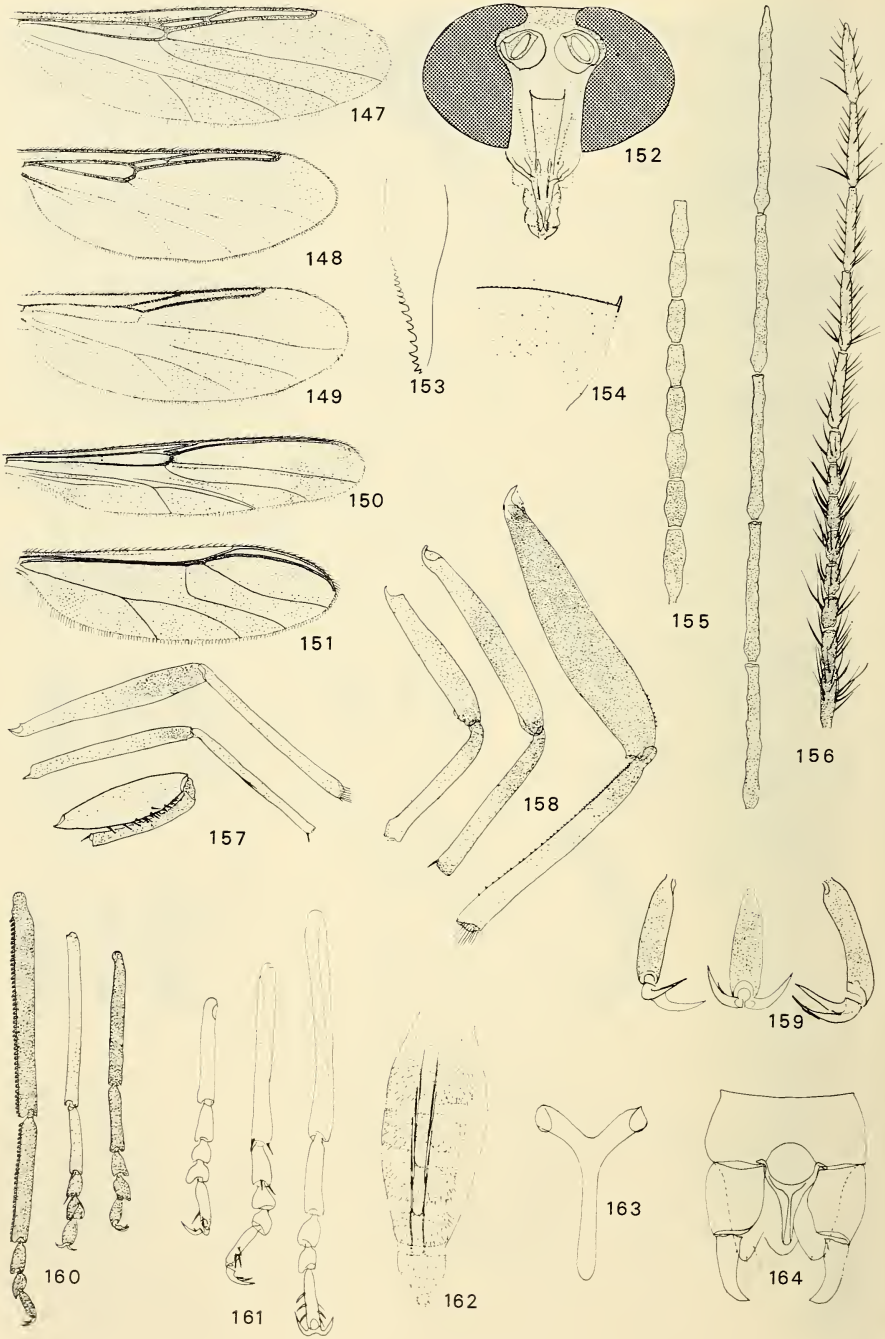
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